ISSN 1346-7565 Acta Phytotax. Geobot. 59 (3): 231-238 (2008)

Adichogamy in *Tricyrtis maculata* and *T. esquirolii* (Liliaceae)

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The flowers and floral phenology in the closely allied *Tricyrtis maculata* (*s. str.*) (Liliaceae) from Nepal and *T. esquirolii* (*s. str.*) from China were compared. The flowers of the two species proved to be adichogamous (homogamous), as their stigmas and anthers mature simultaneously. In *T. maculata*, the practical duration for pollination of each flower is approximately one day. The distal stigmatic branchlets of the style are comparatively short, and the stigmas are conduplicate and open. In *T. esquirolii*, the flowers are open for two days. The stigmatic branchlets are moderately long, and the stigmas are closed along the suture, as in many other species of *Tricyrtis* with dichogamous (protandrous) flowers. The characteristics of the flowers of *T. maculata* as noted above appear to be more advanced than those of *T. esquirolii*. The adichogamous flowers of *T. esquirolii* are presumed to have originated from protandrous flowers.

Keywords: adichogamy, breeding system, dichogamy, floral phenology, homogamy, homoplasy, Liliaceae, pollination system, protandry, *Tricyrtis*

The reproductive aspects of flowers, including pollination mechanisms and breeding systems, have been investigated in various Japanese species of *Tricyrtis* Wall. (Liliaceae) by Takahashi (1984, 1987, 1989, 1994, 1998, etc.). Recently, Tanaka (2008) also reported on some biological features of the flowers of two species of *Tricyrtis*, *T. puberula* Nakai & Kitag. from China and *T. latifolia* Maxim. from Japan. According to these studies, many species of *Tricyrtis* have dichogamous (protandrous) flowers. Only one Japanese species, *T. nana* Yatabe, is known to produce adichogamous (homogamous) flowers (Takahashi 1987, Tanaka unpublished).

Tricyrtis maculata (D. Don) J. F. Macbr. was originally described from Nepal (Don 1825), while *T. esquirolii* (H. Lév.) H. Hara is from Guizhou Province, China (Léveillé 1907). There have been no reports on floral phenology in connection with sexual reproduction in these species. In the course of taxonomic studies of the two species, some interesting observations were made on reproductive characters relevant to pollination and fertilization.

The results of observations of the flowers and the flowering process in the two continental species of *Tricyrtis* are reported, and some related matters are discussed.

Materials and Methods

Circumscription of species

Tricyrtis maculata (*T. pilosa* Wall.) and *T. esquirolii* (*Disporum esquirolii* H. Lév.) were treated as conspecific by Chen & Takahashi (2000). The two species are readily distinguish-

able from each other, however, in several morphological characters, such as hairiness of the leaves and stem, leaf texture, anther length and density of the bladder hairs (or glandular hairs) on the style branches. Further, differences in their sexual reproductive characters were noted during this study, as reported below. The two species are tentatively recognized here as distinct, and are narrowly circumscribed, respectively. The results of my taxonomic studies of the two species and related taxa will be published elsewhere.

Tricyrtis maculata (D. Don) J. F. Macbr. in Contr. Gray Herb. n. s. 53: 5 (1918).

Compsoa maculata D. Don, Prodr. Fl. Nepal.: 51 (1825). —Type: Nepal. *N. Wallich* (n.v.).

Tricyrtis elegans Wall., Tent. Fl. Napal. 2: t. 46 (1826).

Tricyrtis pilosa Wall., Tent. Fl. Napal. 2: 62 (1826).

Compsanthus maculatus Spreng., Syst. Veget. 4 (2): 137 (1827).

Tricyrtis esquirolii (H. Lév.) H. Hara in H. Ohba, & S. B. Malla, Himalayan Pl. 1: 206 (1988), excl. syn.

Disporum esquirolii H. Lév. in Bull. Soc. Bot. France 54: 370 (1907). —Type: China. Kouy-Tchéou [Guizhou]. *J. Esquirol 485* (holotype, E!).

Materials and methods

Living plants of *Tricyrtis maculata* and *T. esquirolii* were examined for this study. *Tricyrtis nana* was also examined for comparison. The plants were cultivated outdoors in the experimental nursery of Teikyo University. Observations of the flowers and the flowering process were carried out in the daytime between ca. 6:30 a.m. and 7 p.m. during the flowering period of each species; late June to early August for *T. maculata* and *T. esquirolii*, and from middle September to early October for *T. nana*. 'Morning' and 'afternoon' refer to daylight hours.

The sources of the materials used are listed below with codes M-1–4 (*Tricyrtis maculata*), E-1 (*T. esquirolii*) and N-1 (*T. nana*). Voucher specimens, including some fragmentary ones in liquid preservative, are preserved in TEU.

Tricyrtis maculata

M-1: Nepal. Arun Valley, top of pass S of Num, in moist shaded oak forest at 2030 m, 21 Sept. 1991, *Edinburgh Makalu Expedition 151*; supplied by Royal Botanic Garden, Edinburgh, Scotland, U.K., accession number 19920048.

M-2: Nepal. *R. J. D. McBeath 2249*; supplied by Royal Botanic Garden, Edinburgh, Scotland, U.K., accession number 19901738.

M-3: Eastern Nepal. Between Chichina and Num on eastern side of Arun River valley, ca. 1750 m, 29 Oct. 1995, *Crûg Farm Plants, U.K., U.S.A., and Heronswood Nursery joint expedition team, designated HWJCM 431*; supplied by Heronswood Nursery.

M-4: Northeastern Nepal. Forests of Mewa Khola, 2200 m, 2002, *Crûg Farm Plants, U.K., and Heronswood Nursery, U.S.A., joint expedition team, designated as HWJK 2411*; supplied by Heronswood Nursery.

Tricyrtis esquirolii

E-1: China. Exact locality unknown, supplied by a Chinese Nursery.

Tricyrtis nana

N-1: Japan. Kyushu. Kagoshima Pref., Shimo-Koshiki Isl., Mt. Odake, 31 May 1988, *N. Tanaka* (s.n.)

Results and Discussion

1) Floral characters

Cultivated plants of both *Tricyrtis maculata* (M-1–4) and *T. esquirolii* (E-1) flower outside from

late June to early August on the campus of Teikyo University in the western suburbs of Tokyo, Japan. Both species develop a terminal cyme and often several axillary cymes on the distal part of the stem. The flowers are held upright (Fig. 1A–D) and are scentless. The tepals are white with pale green on the distal half and with purple (Figs. 1A, 1B) or dark purple maculations (Fig. 1C, D). *Tricyrtis esquirolii* has a faint orangish yellow spot on the subbasal part of the tepals (Fig. 1C), although the spot is often absent on the outer tepals. The yellowish spot is lacking in *T. maculata* (Fig. 1A, B). The outer tepals of both species have a nectary at the base (Figs. 1A–D, 2F, 3A).

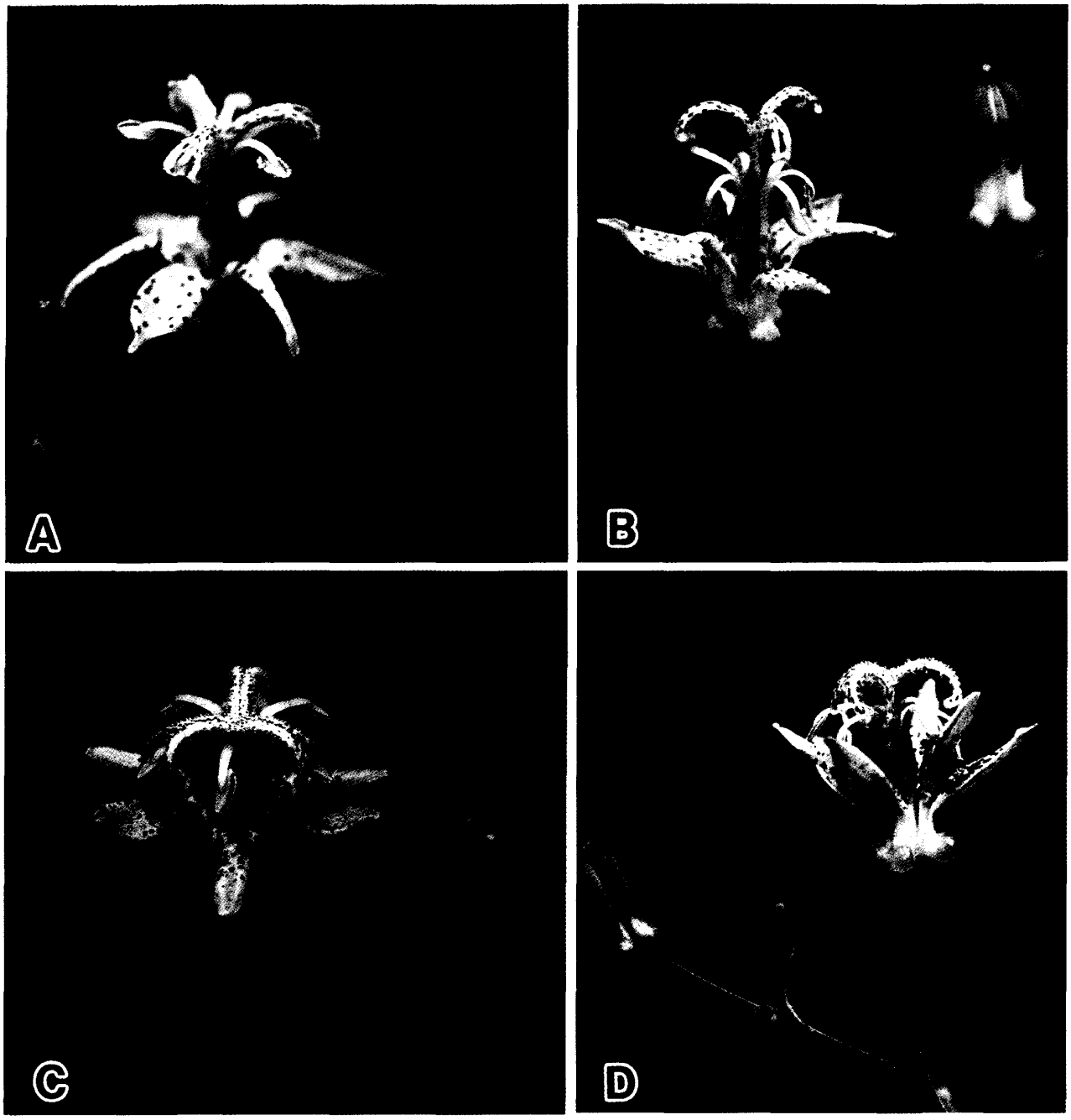

FIG. 1. Flowers of *Tricyrtis maculata* (source M-4) (A, B; same plant) and *T. esquirolii* (source E-1) (C, D; same plant). A: First day flower at 4:20 p.m., 7 Jul. 2006. B: Second day flower with elongate ovary and somewhat faded tepals at 4:15 p.m., 6 Jul. 2006. C: First day flower at 10:10 a.m., 12 Jul. 2006. D: Second day flower with elongate ovary and ascending tepals at 3:15 p.m., 13 Jul. 2006.

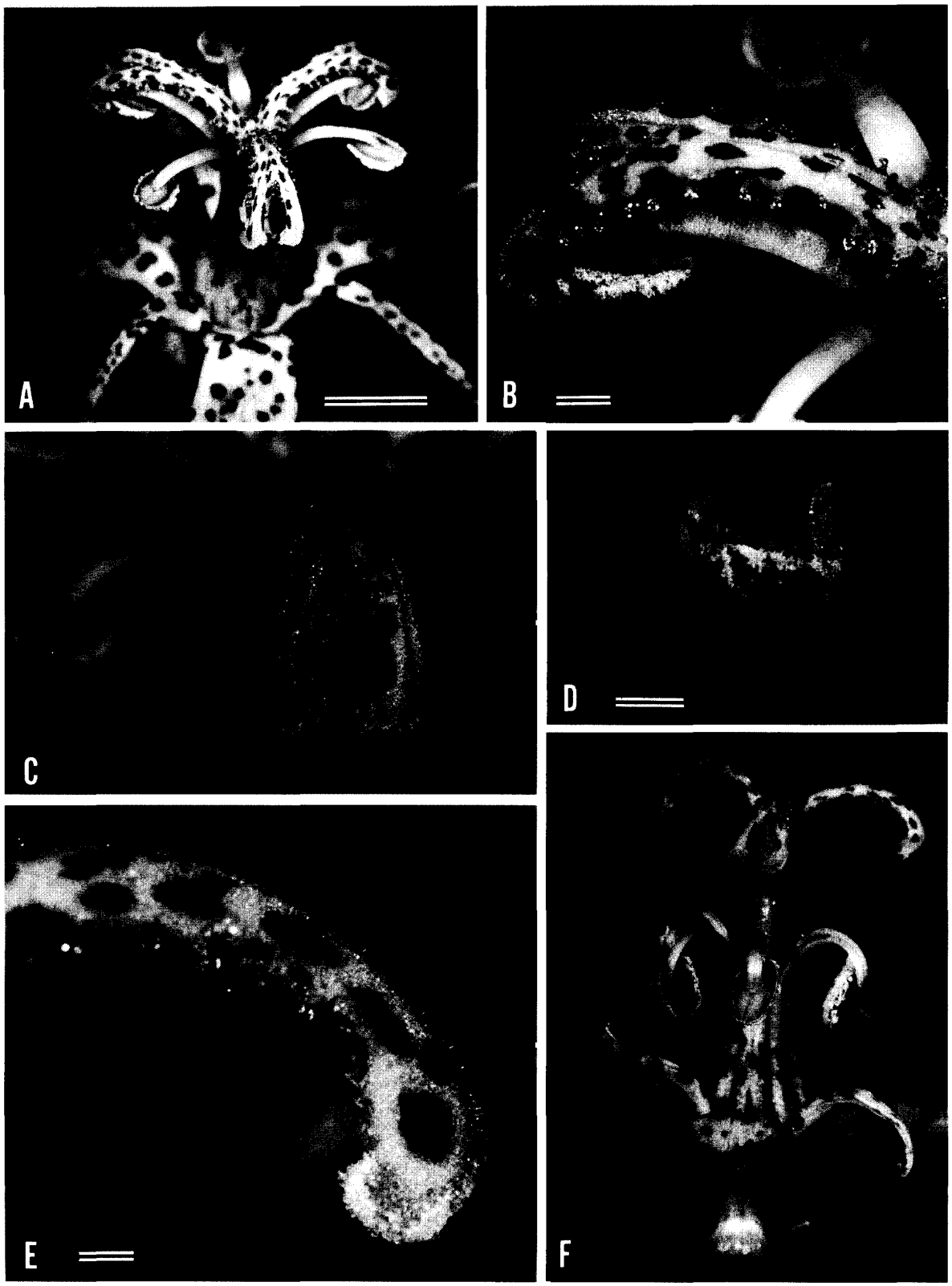

FIG. 2. First day flower (A–E) and second day flower (F) of *Tricyrtis maculata* (source M-4). A: Flower at 3:33 p.m., 8 Jul. 2006. B: Distal stylar branch with mature stigmas and stamens with dehisced anthers; at ca. 3:38 p.m., 8 Jul. 2006. C: Mature stigmas with developed papillae at ca. 3:40 p.m., 8 Jul. 2006. D: Open carpel of mature stigmas and adjacent dehisced anther of outer stamen at 10:15 a.m., 9 Jul. 2006. E: Mature stigma with developed papillae, bearing pollen (side view) at ca. 4:05 p.m., 8 Jul. 2006. F: Flower with elongated ovary, somewhat faded tepals and strongly recurved filaments at ca. 4:00 p.m., 8 Jul. 2006. Scale bars: A & F, 5 mm (at A); B & C, 1 mm (at B); D, 1mm; E, 0.5 mm.

In *Tricyrtis*, the base of the style is simple, distally trifurcate with each branch further bifurcate (Figs. 1–3). In *T. maculata*, the stylar branches are usually 8–9 mm long, including the distal bifurcate branchlets which are ca. 2.5–3 mm long. The stigmas are conduplicately open and somewhat broadened (Fig. 2D, F). The anthers are 3–3.5(–4) mm long.

In comparison, *Tricyrtis esquirolii* has longer stylar branches, 11–12 mm long, including the distal bifurcate branchlets which are (3.5–)4–4.5 mm long. The stigma is closed along the suture, and the stigmatic portion is slender (not broadened) (Fig. 3C). The bladder hairs on the style are more numerous in *T. esquirolii* (Fig. 3A, B vs. Fig. 2A, B in *T. maculata*). The anthers of *T. esquirolii* are usually longer, measuring (3.5–)4–4.5 mm.

2) Flowering process

Tricyrtis maculata

Day before anthesis: Usually in the late afternoon, the flower buds split apically, but anthers remain closed.

Day one of anthesis: In the morning, the anthers are dehiscent with the pollen exposed. The upper branches of the style are recurved with the stigmatic apices directed downward (Figs. 1A, 2A–E). The mature stigmas with fully developed papillae (e.g., Fig. 2E) are positioned close to the anthers, especially those of the outer stamens (Figs. 1A, 2A–D). The tepals are abruptly explanate or recurved from about 1/3 above the base (Figs. 1A, 2A).

Day two of anthesis: In the morning, the ovary is often slightly more elongate (developed) (Figs. 1B, 2F) than on the previous day (Figs. 1A, 2A). The tepals and filaments are slightly faded (Figs. 1B, 2F). The style is similarly faded in the early afternoon. During the daytime, the inner tepals ascend slightly, while the outer ones remain more or less explanate (Figs. 1B, 2F).

Day three of anthesis: The tepals are withered, without change of posture from the previous day. The stamens and the style are also withered. Some floral parts other than the pistil often become detached.

The flowers of *Tricyrtis maculata* are adichogamous, as their stigmas and anthers mature simultaneously on the first day in bloom (Figs. 1A, 2A–E). The recurved stigmatic branchlets of the style and the fully developed stigmatic papillae of the first day flowers of *T. maculata* (Figs. 1A, 2A–E) are comparable with those of the pistillate phase of the protandrous flowers of many other species of *Tricyrtis* (cf. Tanaka 2008). In the staminate phase of the latter, the stigmatic branchlets are usually straight and the stigmatic papillae are significantly smaller and more compact (cf. Tanaka 2008). If the flowers of *T. maculata* are visited by insects or happen to be touched, self pollination may easily occur, as the stigmas and anthers lie in close proximity (Figs. 1A, 2A–D).

The tepals of *Tricyrtis maculata* remain open, even after they become thoroughly withered on the third day, and eventually fall off. Anthesis, therefore, does not end with the closing of the tepals in the plants examined. The functional decline of flowers can be generally estimated by the degree of fading of various floral parts, such as the tepals, stamens and styles. Second day flowers of *T. maculata* initially appear normal, but slight but definite fading is consistently observed in some floral parts as early as the morning of the second day. Fading later becomes more pronounced. These observations may indicate that the practical duration for pollination is nearly one day, although pollination occurring in the early morning of the second day may lead to fertilization.

Tricyrtis esquirolii

Day prior to anthesis: In late afternoon the

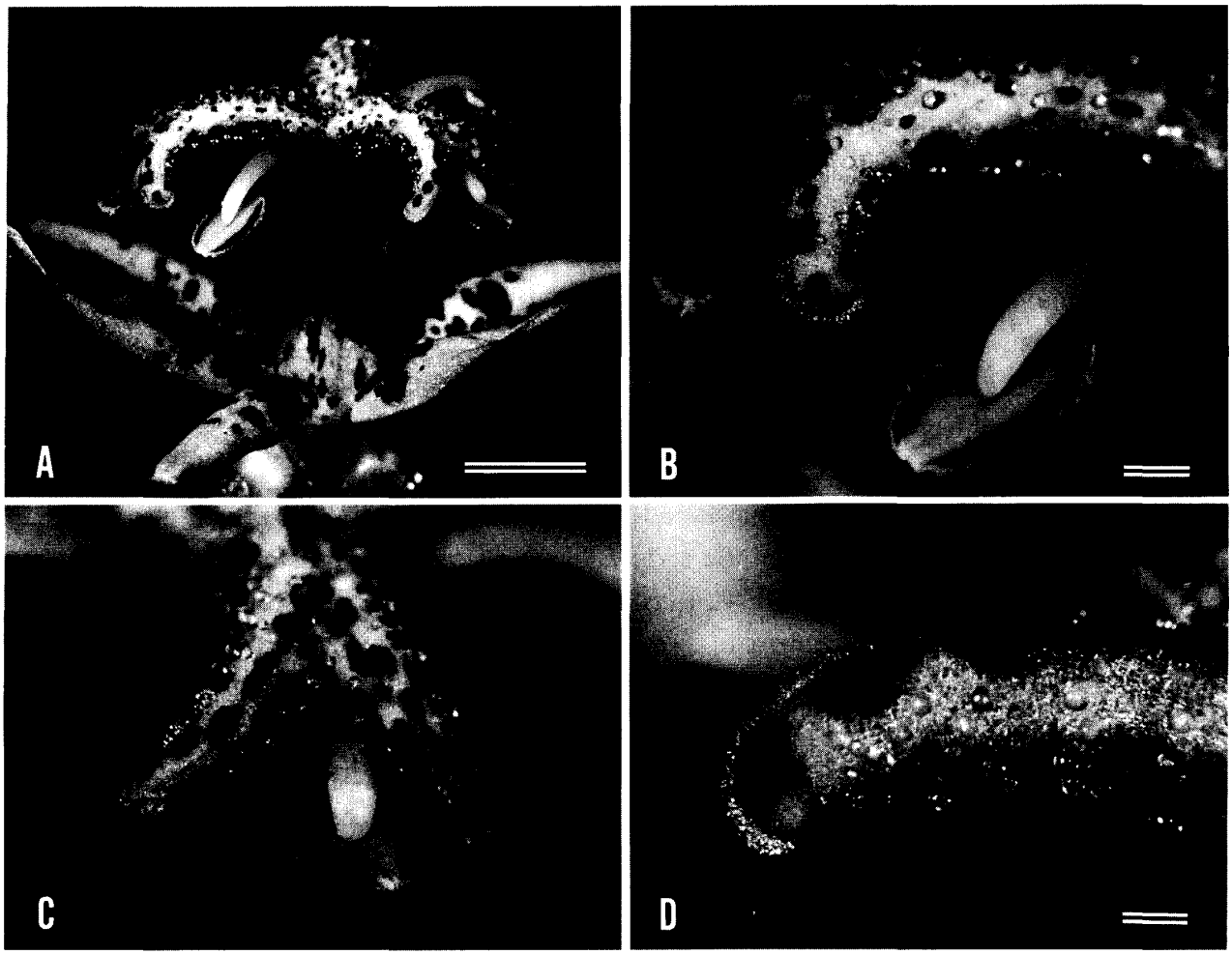

FIG. 3. First day flower of *Tricyrtis esquirolii* (source E-1). A: Flower at 1:36 p.m., 29 Jul. 2006. B: Stylar branch with mature stigmas and two dehisced anthers at 1:40 p.m., 29 Jul. 2006. C: Mature stigmas on distal bifurcate branchlets of style straddling dehisced anther of outer stamen at 2:27 p.m., 29 Jul. 2006. D: Mature stigma with developed papillae (side view) at 10:50 a.m., 15 Jul. 2006. Scale bars: A, 5 mm; B & C, 1 mm (at B); D, 0.5 mm.

flower buds split apically, although the anthers remain closed.

Day one of anthesis: In the morning, the anthers are dehiscent with the pollen exposed. The stylar branches are recurved with the stigmatic apices directed downward (Figs. 1C, 3A–D). The distal bifurcate stigmatic branchlets straddle the anther of the outer stamen (Figs. 1C, 3A–C). The stigmas appear to be mature and receptive, as their papillae are fully developed (Figs. 3B–D).

Day two of anthesis: In the morning, the pistil (ovary) is often slightly more elongate (developed) (Fig. 1D) than on the previous day (Figs. 1C, 3A), as in *T. maculata* (Figs. 1A, 1B, 2A, 2F). During the day, both the inner and outer tepals gradually ascend (Fig. 1D), and eventually become nearly upright toward evening. The tepals show only a faint sign of fading in the late afternoon.

Day three of anthesis: The floral organs other than the ovary are withered. Some tepals and stamens often fall off.

The observations above indicate that the flowers of *Tricyrtis esquirolii* are also adichogamous, as their stigmas and anthers mature simultaneously. The recurved stigmatic branchlets of the style and the fully developed stigmatic papillae of the first day flowers of *T. esquirolii* (Figs. 1C, 3) are similar to those in the pistillate phase

of the protandrous flowers of many other species (cf. Tanaka 2008).

It is also notable that the flowers of *Tricyrtis esquirolii* are in bloom for two days. Apart from being adichogamous, the general floral phenology of *T. esquirolii* is similar to the protandrous flowers that open for two days in other species (cf. Tanaka 2008). In *Tricyrtis*, *T. esquirolii* is the only species where the flowers are adichogamous and are open for two days.

3) Development of adichogamy

Many species of *Tricyrtis* have protandrous flowers lasting for two days. The flowers blooming for two days are staminate on the first day and pistillate on the second day (Takahashi 1984, 1987, 1989, 1994; Tanaka 2008, and unpublished data). Protandry over a two day span of anthesis is probably the basic pollination system in *Tricyrtis*, and this system no doubt promotes cross pollination and outbreeding.

In this survey, the flowers of two continental species, *Tricyrtis maculata* and *T. esquirolii*, proved to be adichogamous. The development of adichogamy (homogamy) may result in self pollination and inbreeding unless self-incompatibility develops. In *Tricyrtis*, there have been no reports of self-incompatibility.

As stated above, in *Tricyrtis maculata*, the flowers appear to be functional for about one day. The stigma is conduplicate and open along the suture (e.g., Fig. 2D), and the distal bifurcate stigmatic branchlets of the style are comparatively short, lying close to the anthers of the outer stamens (Figs. 1A, 2A–D). These features of *T. maculata* appear to be more advanced than those of *T. esquirolii*. The flowers of *T. maculata* are functional for a shorter period, perhaps because of improved efficiency of self pollination. In *T. esquirolii*, in contrast, the flowers are functional for two days (Fig. 1C, D), the stigma is closed along the suture (Fig. 3C), and the distal bifurcate stigmatic branchlets are moderately long (e.g., Fig. 1). These features of *T. esquirolii* are more or less similar to those of many other species of *Tricyrtis* with protandrous flowers (e.g., *T. puberula*, *T. affinis* Makino), implying that the adichogamous flowers of *T. esquirolii* originated from protandrous flowers, and many features of the protandrous pollination system remain. In *T. maculata*, the adichogamous flowers appear to have been derived from an ancestor close to *T. esquirolii*.

Adichogamy in *Tricyrtis maculata* and *T. esquirolii* appears to have developed independently from that of *T. nana* of southwestern Japan. The former two species are apparently remote in affinity and in geographical range from the latter. It is noteworthy that both *T. maculata* and *T. nana* (N-1) developed similar advanced floral characteristics with the development of adichogamy; shortened period of anthesis (about one day) and short stylar branches recurved on the first day of bloom. These may be examples of homoplasy.

The adichogamous flowers of both *Tricyrtis maculata* and *T. esquirolii* retain entomophilous features. For instance, their tepals are spotted purple and the outer tepals have a nectary at the base (e.g., Fig. 1A–D). *Tricyrtis nana* also has reddish purple spots on the tepals and a nectary at the base of the outer tepals. These features are shared by many species with protandrous flowers, which are pollinated principally by bumblebees (e.g., *Bombus diversus*) (Takahashi 1984, 1987, 1989, 1994, 1998). Visitations by such pollinators may still be effective, even in species with adichogamous flowers. The flowers of *T. nana* are visited by insects and are effectively pollinated by *Bombus diversus* (Takahashi 1987).

To elucidate the evolutionary process of adichogamy in *Tricyrtis maculata* and *T. esquirolii*, further investigations on plants from more localities, and on natural populations, are needed.

A taxonomic revision of *Tricyrtis maculata* and *T. esquirolii* is also needed. If the two species

are united, the variation in adichogamy will necessarily be regarded as intraspecific variation.

I am most grateful to the Director of the Royal Botanic Garden, Edinburgh, Scotland, U.K., for providing living plants of *Tricyrtis*. I also thank the Keeper of the herbarium (E) for the loan of specimens, Mr. Bleddyn Wynn-Jones, Crûg Farm Plants, Wales, U.K., for the collection data of some plants of *T. maculata* from Nepal, and Dr. David E. Boufford at Harvard University, U.S.A., and two anonymous reviewers for their helpful suggestions on my manuscript.

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Received February 5, 2008; accepted September 22, 2008